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Use of individual colour-ringing to estimate annual survival in male and female Red Knot *Calidris canutus islandica*: a progress report for 1998–2001

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In relatively long-lived birds like shorebirds, even small changes in adult mortality may affect population size. However, annual survival estimates based on metal-ringing and accumulating recoveries by the general public take at least a decade to materialise. To try and obtain faster and more sensitive estimates of annual survival, we started an individual colour-ringing project on Red Knots *Calidris canutus* in 1998, focusing on the *islandica*-subspecies that spends part of the non-breeding season in the Dutch Wadden Sea. By using molecular sex determination techniques we were able to distinguish males and females. A total of 1805 birds was colour-marked in the study period from August 1998 to late 2001. Of these, 1603 were adult birds (52% were female, 39% male and 9% undetermined). Based on a total of 850 individual observations, 486 different adults were resighted at least once over this period. Using the software MARK, we estimated average annual survival in adult birds as 0.841 (SE = 0.066). Compared with previous studies this is a great improvement in the time over which a survival estimate can be obtained with such precision. No differences between sexes and years were apparent.

INTRODUCTION

Survival rate is a key variable in population dynamics. In migrating shorebirds, survival may be correlated with the length of the migrations (Piersma 1994) and with breeding success (Boyd & Piersma 2001a). Red Knots breed in the High Arctic and are long distant migrants. They have proven to be a good model species of a long-distance migrating shorebird with a well described migration system (Piersma & Davidson 1992). Since 1960, Red Knots have been metal-ringed in the British estuaries, and an analysis of survival based on almost 88,000 ringed individuals and their recoveries is now available (Boyd & Piersma 2001a). It appeared that the survival estimates were not very precise, and that many years of data-gathering are required to accumulate sufficient recaptures and recoveries to be able to say anything at all.

In view of fast human-induced changes occurring in the European coastal wintering areas of Red Knots (e.g. Piersma *et al.* 2001, Camphuysen *et al.* 2002), it seemed important to obtain survival estimates over shorter time intervals than a decade or so. In 1998, the shorebird research group at the Royal Netherlands Institute for Sea Research (NIOZ) on Texel started an individual Red Knot colour-ringing project in the Dutch Wadden Sea. Here we provide a first assessment of the effectiveness of this system in getting survival estimates. A parallel development was the possibility to determine the gender of individual Red Knots with certainty using a molecular technique (Baker *et al.* 1999). This enabled us to test for sex differences in survival as well.

MATERIAL AND METHODS

Red Knots were mistnetted near important high tide roosts in the Dutch Wadden Sea, especially the islets Richel (53.17°N, 5.08°E) and Griend (53.15°N, 5.16°E) and the island Schiermonnikoog (53.29°N, 6.15°E). Birds received a metal ring, a unique combination of four colour rings (blue, red, white and yellow) and a yellow flag. The colour rings were always put on the tarsus (two each) and in addition there were eight different possible flag positions (on either tibia, and on top, between and below the two colour rings on either tarsus). To ensure readability of the colour-rings, only the three primary colours (yellow, red and blue) plus white were used. These were of 'Darvic' plastic and supplied by A.C. Hughes LTD, Middlesex, England. We used Marley Solvent Cement to permanently close the flag and the colour rings. Of a total of 4^4 times 8 = 2048 possible combinations, 1805 combinations were used up to the end of 2001.

In addition to colour-ringing, information on primary and body moult, plumage status, body mass and biometric data were gathered . We also collected a small blood sample from the capillary vein to determine sex using a verified molecular technique (Baker *et al*. 1999). Birds were aged as juveniles (in their first year of life) or adults on the basis of plumage characteristics. Of the 1805 birds ringed from 1998 to 2001, 11.2% were juveniles. These are not included in the present analysis. In addition, we restricted our analysis to birds belonging to the *islandica* subspecies. A total of 83 Red Knots was assigned to the West-African wintering *canutus* subspecies on the basis of timing (captured in July or August), absence of wing moult, and body mass (birds weighing more than 150 g during this time of year are fueling for onward flight) (see Nebel *et al.* 2000 and Boyd & Piersma 2001b for more information on these criteria).

In the field, we repeatedly tried to identify colour-ringed birds with 20–60× zoom-telescopes. Colour-rings could be observed best when the flocks allowed approaches to within 100 m and in good weather (winds stronger than Beaufort force 5 made observations very difficult, as did rain). Most field observations were made in the western half of the Dutch Wadden Sea. The use of a yellow flag, which almost always was picked up first during field observations, reduced the likelihood of bias in resighting particular colour-ringed combinations. In fact, an analysis of the resighting table suggests such a bias to be absent.

The past twenty years has seen enormous development of increasingly sophisticated and user-friendly software to analyse survival (SURVIV (White 1983), SURGE (Lebreton & Colbert 1986) and MARK(White & Burnham 1999)). We used MARK, which is a particularly user-friendly package that incorporates many demographic modelling tools (http://www.cnr.colostate.edu/~gwhite/mark/mark.htm). Because our data consist of resightings/recoveries, we used the Cormack-Jolly-Seber (CJS) model. The CJS model can account for differences in survival rates between successive time periods, in our case calendar years (Lebreton *et al*. 1992). For the analyses, one needs to compile a 'life history' for each colour-ringed individual. This consists of a sequence of 'zeros' or 'ones'. If a bird is sighted within a particular calendar year it receives an '1'; if it is not seen in a year it receives a '0'. The 'life history' starts with a '1' in the year of ringing. For example, a bird ringed in 1998 and resighted in 1999 and 2001 only, will have a 'life history' that reads '1101'.

On the basis of these individual resighting histories MARK calculates a 'recovery' rate, or actually, a resighting rate (p; the likelihood that a living individual is actually resighted within a given period) and a survival rate (phi = ϕ; the likelihood that a given individual has not left the population or is not dead). Four different versions of the CJS model were examined, differing in the extent to which survival and resighting rates were held constant (indicated with Phi(.) and p(.), respectively) or whether they were considered year-dependent (indicated with Phi(t) and p(t), respectively). The results were corrected for slight overdispersion of the data using the value of the goodness of fit parameter c-hat (based on 100 bootstraps) of 1.28 (see web-based manual to MARK, chapter 5).

Akaike's Information Criterion (AIC; Anderson & Burnham 1999 a, b) was used to determine the version of the CJS model that gave the best fit to the data. As more parameters are included in the model, the fit obviously gets better. However, with more parameters the complexity of the model also goes up, and the precision of the estimates of individual parameters goes down. AIC is a statistic to find a balance between fit and precision. When the AIC-Weight is highest, the balance between fit and precision is optimal.

RESULTS

In the period 1998–2001, 1,603 adult *islandica* were individually marked, of which 486 were subsequently resighted at least once (Table 1). The 1,603 adult colour-ringed Red Knots consisted of 52% females, 39% males and 9% undetermined sex. The latter category consists of birds for which the DNA analysis is not yet done or for which the blood sample was damaged or lost. MARK indicated that there were no differences in survival rate between the sexes (Likelihood Ratio Test, p = 0.490).

In the absence of differences in survival between the sexes, the combined dataset was used to estimate overall survival rate. According to the values of AIC-Weight, the best model is Phi(.) p(t), which means that the best fit with the data is obtained when survival is considered constant between years and when resighting rates are year-dependent (Table 2). An annual survival rate of 0.841 (SE = 0.066) over the whole period was then calculated (Table 3). Because the resighting rate 'p' was a time-dependent factor, the three yearly resighting rates ranged from 0.145 to 0.200.

DISCUSSION

Between 1998 and 2001, the average annual survival rate of adult colour-ringed Red Knot was 0.841. This value is within the range of estimates made by Boyd & Piersma (2001a),

Table 1. Resighting matrix for adult *islandica*-Red Knots colour-ringed in the Wadden Sea from 1998–2001.

Year	n_{ringed}	$n_{resighted}$				Total $n_{resighted}$
		1998	1999	2000	2001	
1998	236	30	42	19	36	99
1999	555	–	101	70	74	202
2000	225		–	19	36	52
2001	587			–	133	133
Totals	1603					486

Table 2. Results of the survival analysis on a year basis of Red Knots between 1998 and 2001. Parameters: 'phi' = survival rate; 'p' = resighting rate. Conditions: '.' = constant parameter; 't' = time-dependent (annual) parameter. The analysis used a c-hat overdispersion correction factor of 0.8958.

Model	AICc	Delta AICc	AICc Weight	No. of parameters	Deviance
Phi(.) p(t)	1811.7	0.00	0.530	4	8.96
Phi(t) p(t)	1813.7	2.02	0.193	5	8.96
Phi(t) p(.)	1813.8	2.15	0.181	4	11.11
Phi(.) p(.)	1815.1	3.44	0.095	2	16.42

Table 3. Parameter estimates for the best fit model phi(.) p(t) for adult Red Knot over the period 1998–2001 based on the analysis presented in Table 2.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
Survival (1998–2001)	**0.841**	0.066	0.670	0.937
Resighting rate (1998–1999)	0.196	0.030	0.143	0.262
Resighting rate (1999–2000)	0.145	0.019	0.111	0.188
Resighting rate (2000–2001)	0.200	0.033	0.143	0.273

from 0.61 in the period 1960–1968 to 0.87 in the period 1977–1985. Encouragingly, the precision of the survival estimate based on three years of resighting data (SE = 0.066) is of the same order of magnitude as the precision of the overall average survival estimate of 0.74 based on 36 years of metal-ringing (SE = 0.013). This is obviously a consequence of the much greater 'recovery' rate using colour-ringing. For Red Knots metal-ringed in Britain between 1960 and 1995, an overall average of 2.32% were recovered (Boyd & Piersma 2001a). The 35% resighted within the first three years of this project certainly compares favourably (NB: within this period only a handful of the usual metal-ring recoveries were accumulated).

The between-year differences in resighting rate (Table 3) are due to differences in observer effort. Systematic fieldwork was carried out during a longer period in 2001. Between July and December 2001, C.B. spent 146 hours on fieldwork and read 279 colour-rings, or about 1.9 colour-rings per field hour. Colour-ringing plus a good resighting effort greatly enhances the effectiveness of any shorebird ringing programme. The present study was based on roughly 6000 working hours to catch and ring Red Knots. This effort was followed up with about 500 hours searching for birds with colour-rings. For more precise annual survival rate estimates, a better balance between the efforts of catching and ringing on the one hand and of making resightings on the other, is required.

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